

PREDATION ON RECENT TURRITELLINE GASTROPODS FROM THE INDIAN SUBCONTINENT AND COMPARISON WITH A REVISED GLOBAL DATABASE

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ABSTRACT

Traces of predation by drilling gastropods and peeling crabs provide important insights about predator-prey interaction in ecological as well as evolutionary times. Predation on turritelline gastropods, in this context, has been frequently discussed in literature. Here, we have estimated the intensity of predation (both drilling and peeling) on Recent turritelline gastropods from the Indian subcontinent, which has been underrepresented in previous studies. Our samples include our own collections from several Indian coasts as well as a vast collection which was locked in the archive of the Zoological Survey of India (ZSI) in Kolkata for the past 150 years. It includes samples from different parts of the Indian subcontinent as well as from many other countries. Drilling frequency (DF) of Indian turritelline species is low compared to average values of global data. We suggest that this is mainly because most of the Indian species are larger (> 4 cm) than species living elsewhere. Smaller species show higher DF and lower values of peeling frequency. Size selectivity of drill holes shows both intra- and interspecific variation. Shell thickness and ornamentation appear to be antipredatory in nature.

We have compared our results with a revised global database. Distribution of intensity of predation shows latitudinal variation where both drilling and peeling frequencies increase towards the tropics.

Key words: turritelline prey, drilling predation, peeling predation, Indian subcontinent, global dataset.

INTRODUCTION

Predation pressure exerted by a diverse group of drilling gastropods and durophagous crabs (for example, the calappids) has been identified as an important agent of selection that affects the distribution and abundance of prey community in modern marine ecosystems (Vermeij, 1977, 1987; Stanley, 2008). Traces of this kind of interaction (e.g., drill holes and repair scars) provide abundant information regarding predator-prey dynamics (Kowalewski, 2002), which can be used to test evolutionary hypotheses like enemy-driven adaptation, that is, escalation (Vermeij, 1987; Kelley & Hansen, 1993, 1996; Dietl & Alexander, 2000).

Several attempts have been made to assess tempo and mode of drilling and peeling predation since the Cretaceous (Vermeij, 1987; Allmon et al., 1990; Kowalewski et al., 1998; Walker et al., 2002; Harper, 2006), the time when many marine predators evolved and diversified (reviewed in Walker et al., 2002). These predators include the two most

diverse, modern predatory drilling gastropod families, Naticidae and Muricidae (Sohl, 1969; Taylor et al., 1983). The available methods for quantification of drilling and peeling frequencies are controversial. There are two major estimates of predation intensity. Assemblage-level study estimates overall predation intensity of the entire fossil assemblage including all, or “frequently attacked” taxa (Kowalewski, 2002). In contrast, the lower taxon frequency (LTF) estimates taxon-specific (e.g., species, genus, or family) predation intensity. Compared to assemblage-level studies, the taxon-level predation analysis is biologically and ecologically more meaningful. This is because predators may show prey preference (for example: Bardhan et al., 2012), which may be explained by cost-benefit analysis, prey availability, or prey palatability. Incorporating certain taxa which are never attacked in the analysis will make the result misleading as a measure of overall predation intensity. For this reason, the LTF may be a good way to analyze the dataset (Kowalewski, 2002). Moreover, different spe-

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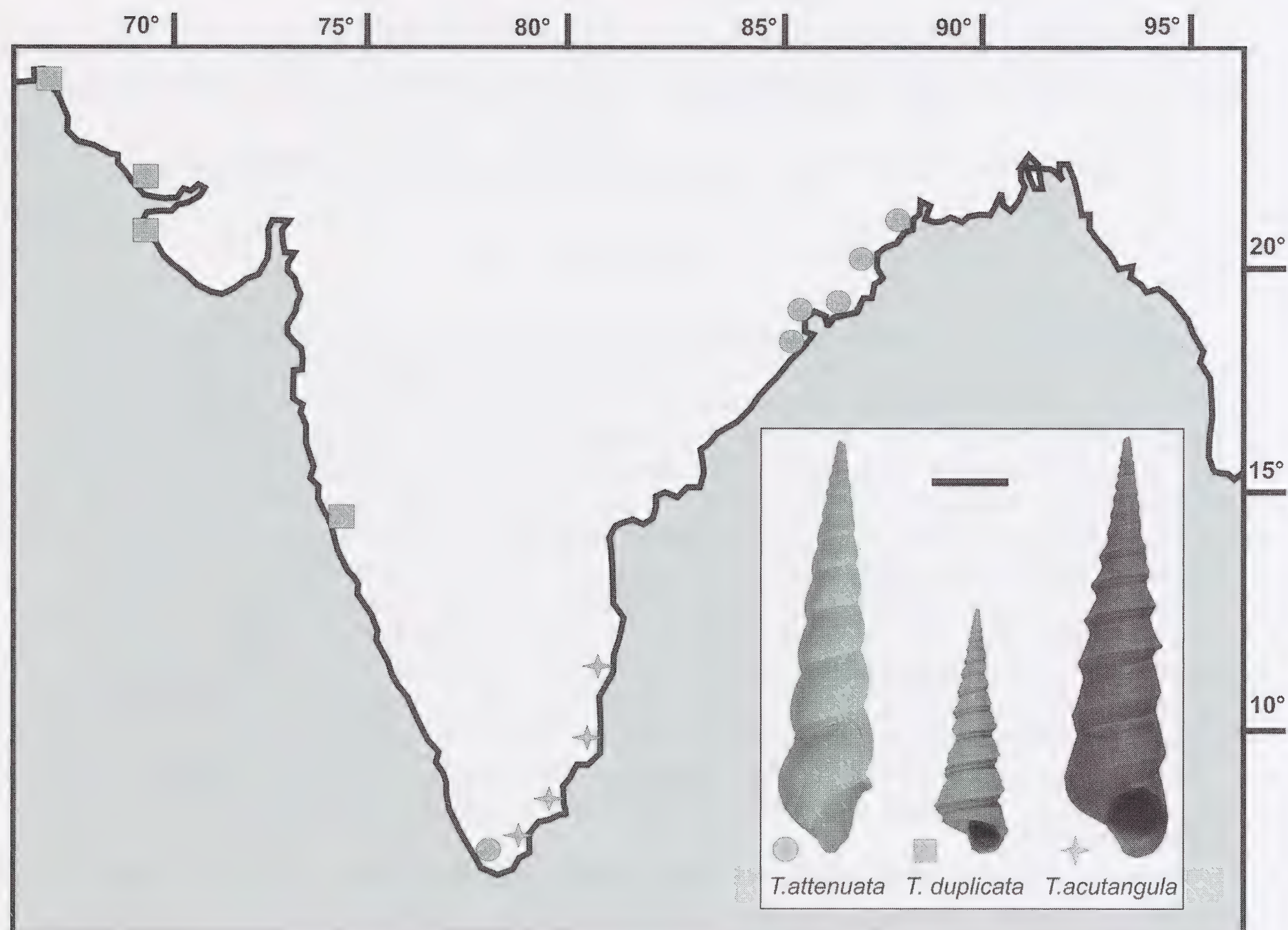


FIG. 1. Biogeographic distribution of the three abundant turrnelline species on the Indian coast (modified after Paul & Das, 2011). Scale bar = 2 cm.

cies can have differential preservation; the LTF is mostly free of this kind of taphonomic bias (Vermeij, 2002).

Turrnelline gastropods are important prey taxa for naticid drilling predation and have ubiquitous fossil record since the Cretaceous (Dudley & Vermeij, 1978; Allmon et al., 1990). It is a well-studied group and spatiotemporal distribution of naticid drilling frequency in this group has been well established (Dudley & Vermeij, 1978; Allmon et al., 1990). However, previous works on Recent turrnelline predation have been based on data mainly from the U.S.A. and western Europe (Dudley & Vermeij, 1978; Allmon et al., 1990; Gerhard et al., 1997), and Indian examples are either sparsely cited or lacking altogether. Living Indian turrnelline species are diverse ($n = 13$; Subba Rao et al., 1991, 1992; Subba Rao & Dey, 2000; Subba Rao, 2003, and personal observation). Among them the three most abundant species – that is, *Turritella attenuata* (Reeve 1849), *T. duplicata*

(Linnaeus 1758) and *T. acutangula* (Linnaeus 1758) – live allopatrically in three different coastal regions of mainland India with minor geographic overlap (Fig. 1). The present studied samples have been collected from different coasts (7,157 km coastline) along the Indian subcontinent and islands. The majority of the samples were collected by British workers before the independence of India in 1947 and are now archived in the Zoological Survey of India (ZSI), Kolkata. This collection also includes species from nearby countries (e.g., Myanmar, Sri Lanka and Pakistan). As far as we know, no data on predation on turrnellines has previously been reported from these regions. All these reasons have prompted us to use these data locked in the ZSI repository for about 150 years to make a new estimate of intensity of predation on turrnelline gastropods from Indian subcontinent, and to make a comparison with data from other parts of the world, using the LTF method.

MATERIAL AND METHODS

The material used for the present study came from two sources: (1) the collections archived in the ZSI (ZSI samples, marked as ¹ in Table 1), and (2) our own collections (marked as ² in Table 1) from different coastal regions of India, repositied in the Museum of the Department of Geological Sciences, Jadavpur University, Kolkata. ZSI samples were mainly collected by British workers before 1947 from several parts of the Indian subcontinent as well as from other parts of the world.

Old museum collections may be fraught with potential bias (discussed in Allmon, 2005). Many collections may be donated by amateurs and non-specialists, which may lead a bias towards large size and good preservation. The present ZSI collections were made by different survey parties and identified by the experts present in the ZSI (Dey, pers. comm., 2013). The experts included British malacologists who carried out systematic works on turritellines and other gastropods (e.g., Smith, 1878; Nevill, 1884; Melvill & Standen, 1889). However, we have made a thorough systematic revision of

this collections based on recent literature. Most of the species are represented by specimens of varied size and condition (intact and broken, and including corroded shells). For example, in *T. acutangula*, out of 75 specimens about 9.3% (7 specimens) and in *T. duplicata*, out of 138 specimens about 12.3% (17 specimens) shells are broken. In broken specimens, apical parts consisting of two to three whorls are missing, and in other cases outer whorls are either absent or apertural margins are broken.

Systematics of the family Turritellidae is in a state of flux (Allmon, 2011). Although the family Turritellidae is considered a monophyletic group, its phylogenetic relationship with other families within the Cerithioidea is not well understood. The subfamilies within Turritellidae are not unanimously accepted, and their monophyletic nature within the family remains unclear (Allmon, 2011). There are many genera that are not now considered as turritellines (e.g., *Mesalia*; Squires & Saul, 2007). The genus *Turritella* itself is virtually a “catch-all” genus, and many *Turritella* species have been grouped into other genera (Allmon, 2011). For our work, we have made some systematic revi-

TABLE 1. Data on drilling (DF) and peeling (PF) frequencies in living turritellines from India, Indian subcontinent, and other parts of the world. Size classes of species have been made following Dudley & Vermeij, 1978. ¹Samples are archived in the ZSI (Zoological Survey of India). Most of the locality names are mentioned in the ZSI register, but in some cases, localities are labelled as “Unknown” or “Eastern sea”. Eastern sea may refer to either east coast of India or eastern Pacific (Dey, pers. comm., 2013). ²Personal collections repositied in the Department of Geological Sciences, Jadavpur University, Kolkata. “n” denotes specimen numbers, *denotes systematic revision of the species name based on Paleobiology database (19/12/2012).

Species / Locality	Length < 4 cm			Length > 4 cm		
	n	PF	DF	n	PF	DF
<i>Turritella attenuata</i>						
Madras ¹	3	0.33	0%	20	2.85	0%
Chandipur ²	6	1	66.7%	424	1.62	18.16%
Digha ²	2	2	50%	327	2.57	11.92%
Eastern sea ¹	0	0	0%	4	8.25	0%
Unknown ¹	0	0	0%	5	6.2	0%
Cape Comaron ¹	0	0	0%	1	3	0%
Goa ¹	0	0	0%	2	2.5	0%
Pondicherry ¹	0	0	0%	2	3	0%
Tranquebar ¹	5	1.6	20%	4	1.75	0%

(continues)

(continued)

Species / Locality	Length < 4 cm			Length > 4 cm		
	n	PF	DF	n	PF	DF
<i>Turritella duplicata</i>						
Goa ¹	3	0	0%	25	1.36	0%
Okha ¹	0	0	0%	1	3	0%
Gulf of Kutch ²	74	0.72	16.21%	3	2.67	0%
Nayabazar, Bedi ¹	0	0	0%	1	1	0%
Madras ¹	3	0.67	0%	12	3.08	0%
Rangoon ¹	1	0	0%	4	1	0%
Persia ¹	33	0.55	33.3%	3	0.67	33.3%
Baluchistan ¹	51	0.37	9.8%	0	0	0%
Dwarka ²	35	0.69	34.3%	7	1.28	0%
Ceylon ¹	0	0	0%	1	1	0%
<i>Turritella acutangula</i>						
Madras ¹	20	0.1	5%	15	1.33	6.67%
Pondicherry ¹	1	0	0%	9	1	0%
Mallipattinam ¹	0	0	0%	2	2	0%
Arabian coast	0	0	0%	2	2	0%
Kakinada ¹	0	0	0%	2	3	0%
Rameswaram ¹	0	0	0%	3	1	0%
Gulf of Mayanmar	1	0	0%	2	1	0%
Goa ¹	0	0	0%	8	1.25	0%
Chilka Lake	3	0	33.3%	2	0.5	0%
Tutikorin ¹	5	0	40%	0	0	0%
<i>Turritella bacillum</i>						
Rangoon ¹	2	0.5	0%	0	0	0%
<i>Turritella terebra</i>						
Eastern Sea ¹	0	0	0%	5	4	0%
<i>Turritella columnaris</i>						
Ceylon ¹	4	2.5	25%	4	6.5	50%
Okha ¹	1	0	0%	6	1.83	16.7%
Unknown ¹	30	0.4	20%	2	3	0%
<i>Turritella (Haustator) trisulcata</i>						
Tamilnadu ¹	19	0.16	15.7%	0	0	0%
Subramannium temple ¹	10	0.3	30%	0	0	0%
Baluchistan ¹	7	1.14	28.6%	3	2	0%
<i>Turritella nebulosa</i>						
Madras ¹	0	0	0%	1	0	100%
<i>Turritella capensis</i>						
False Bay (Andhra) ¹	4	0.5	0%	0	0	0%

(continues)

(continued)

Species / Locality	Length < 4 cm			Length > 4 cm		
	n	PF	DF	n	PF	DF
Cape of Good Hope ¹	6	0.33	0%	0	0	0%
False Bay ¹	10	0.3	20%	0	0	0%
<i>Turritella fascialis</i>						
Muscat ¹	14	0.21	35.7%	0	0	0%
Gulf of Oman ¹	12	0	41.7%	0	0	0%
<i>Turritella vitullata</i>						
China ¹	7	0.43	0%	0	0	0%
Persian Gulf ¹	6	1	0%	4	1.25	25%
<i>Colpospira sinuata</i> *						
Australia ¹	9	0.89	22.2%	0	0	0%
Unknown ¹	5	0.6	40%	0	0	0%
<i>Turritella carinifera</i>						
Cape of Good Hope ¹	13	0.77	7.7%	4	4	0%
<i>Turritella nivea</i>						
Baluchistan ¹	22	0.28	13.6%	1	1	0%
Persian Gulf ¹	6	0	0%	1	0	0%
<i>Archimediella fastigiata</i> *						
Andaman ¹	5	0.4	0%	2	1.5	50%
Margui Archipelago ¹	2	1	50%	0	0	0%
<i>Turritella infraconstricta</i>						
Andaman ¹	5	0.8	0%	1	1	0%
<i>Turritella (Haustator) monilifera</i>						
Andaman ¹	0	0	0%	1	3	0%
<i>Maoricolpus rosea</i> *						
New Zealand ¹	6	1.67	0%	6	1.5	0%
<i>Turritella variegatus</i>						
West Indies ¹	0	0	0%	5	3.6	0%
<i>Turritella fuscocincta</i>						
Australia ¹	31	0.26	0%	0	0	0%
<i>Turritella hanleyana</i>						
Ceylon ¹	0	0	0%	1	9	0%
<i>Turritella communis</i>						
England ¹	4	2	0%	4	2.75	0
<i>Turritella exoleata</i>						
West Indies ¹	18	0.5	0%	0	0	0%
<i>Archimediella maculata</i> *						
Aden ¹	5	1.8	20%	3	1.33	66.7%

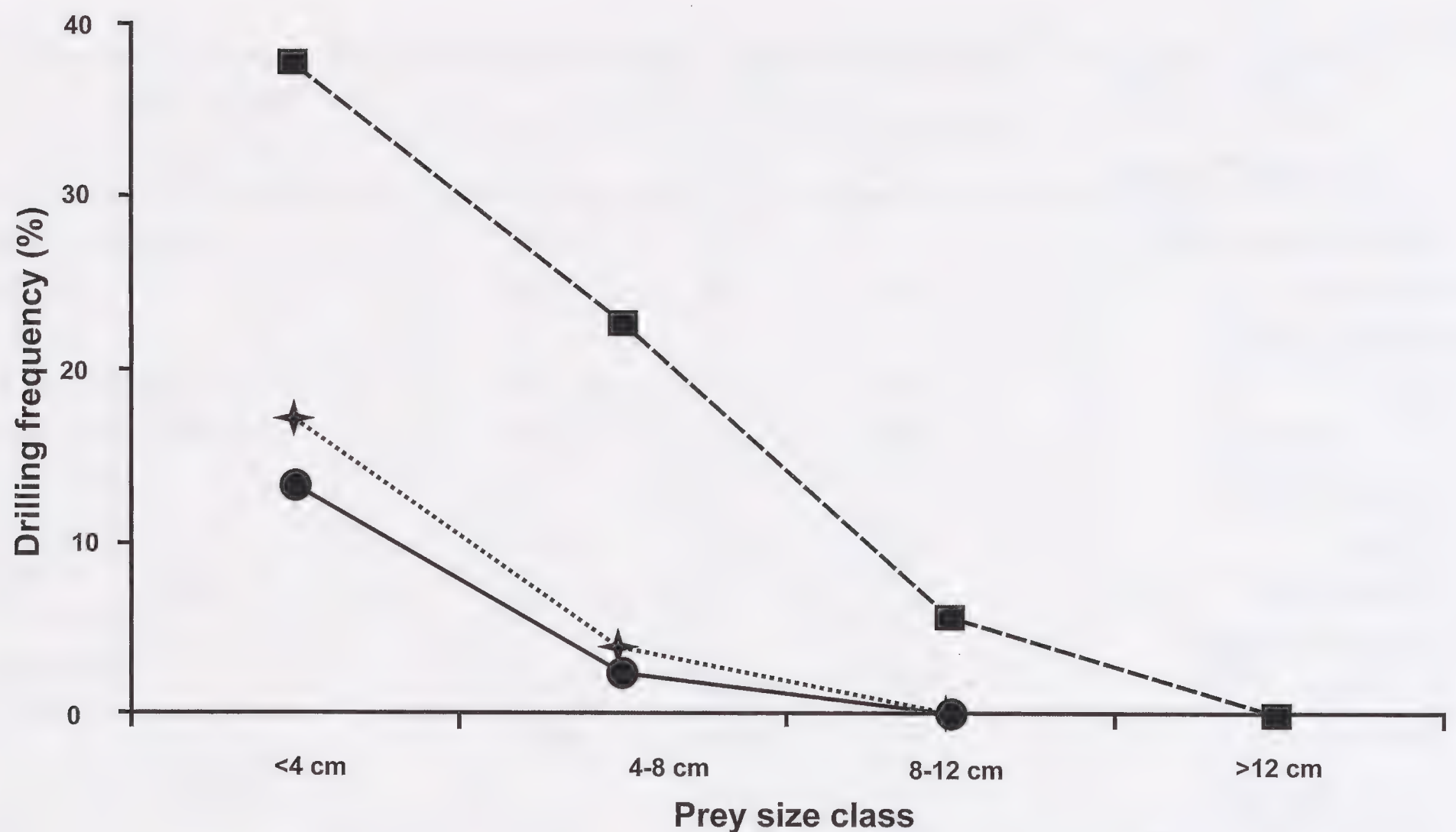


FIG. 2. Frequency of naticid drill holes for four different size classes in three abundant Indian species. Note a fall in DF during ontogeny of all species. Symbols: squares: *T. attenuata*, stars: *T. duplicata*, circles: *T. acutangula*.

sion of some species, based on consultation with taxa listed in the Paleobiology Database (www.pbdb.org). For example, one species that has been labelled as *Turritella fastigiata* in the ZSI collections has now been designated as *Archimediella fastigiata* (for other revised species: Table 1). Identification of most of the present turritelline species are based on recent monographs published by Zoological Survey of India (Subba Rao et al., 1991, 1992; Subba Rao & Dey, 2000; Subba Rao, 2003). The three main Indian species, namely, *T. attenuata*, *T. duplicata* and *T. acutangula*, are taxonomically stable and have been reported also from other parts of the world (Allmon, 2011; Waite & Strasser, 2011). *Turritella capensis* has been previously wrongly labelled as *T. "knyonaensis"*. We have now corrected it in the register of ZSI collection.

Although there is no way to know with certainty what biases affected the collecting represented by the ZSI specimens, circumstantial information suggests that we may use them for present purposes with some confidence. For example, the distribution of smaller and larger size classes in both ZSI and our new collections are comparable, which indicates that the ZSI collections for *T. attenuata* are not biased towards larger size classes. Many ZSI species

show high frequencies of drilling or peeling (Table 1). For example, drilling frequency or DF, a measure of how frequently a species has been drilled by gastropods, on *Archimediella fastigiata* and peeling frequency or PF, a measure of how frequently a species has been peeled by crabs and subsequently repaired, on *T. duplicata* in the ZSI collection are both high, suggesting that drilled or peeled specimens were not excluded from ZSI collection.

In addition, the present study includes only 576 ZSI specimens (40% of the total specimens considered), and data from these specimens may show substantial differences from specimens in our own collection. For example, *T. attenuata* collected by us has DF which varies between 50%–67% in smaller specimens, whereas in ZSI collection, DF varies from around 0%–20% in the same size class. This may be the artefact of low sample size of ZSI collections (Table 1). When sample sizes are large (e.g., *T. duplicata* from Persia, $n = 33$ in ZSI collection and Dwarka, $n = 35$ and Kutch, $n = 74$ in our own collection), drilling frequencies are very similar (Table 1). We do not claim that DFs are invariant in a spatial framework; indeed, previous work has shown that a species may show spatial variability in predation intensity (Leighton, 1999; Dietl & Kelley, 2001;

Harries & Schopf, 2007; Martinelli et al., 2013). Therefore, we argue that, at least for our purposes, although old museum collections are potentially biased, they are usually better than nothing, especially for completely unreported data in a neglected region of the world, such as India (Allmon, 2005; pers. comm., 2012).

Our own collections were made from several localities along the eastern (Chandipur, Orissa; Digha, West Bengal; $n = 759$) and western coasts (Gulf of Kutch and Dwarka, Gujarat; $n = 119$) of India (Fig. 1), from two consecutive field trips during 2010 and 2011. These have enabled us to study spatial variation of predation on modern turritelline clade for which predation data are available from other areas. About 1,454 complete or nearly complete shells, including the ZSI material, were examined to record two types of predation marks (drill holes and repair scars). We have also compared our present data with a revised global data set (taken mainly from Buchanan, 1958; Dudley & Vermeij, 1978; Tull & Bohning-Gaese, 1993; Gerhard et al., 1997; Sawyer & Zuschin, 2010). Since predation frequency varies with prey size, we have measured it for different size classes. For the global dataset, only two size categories were compared – < 4 cm versus > 4 cm (Table 1). For three most abundant Indian species, detailed analyses were done by classifying them in four size-categories (i.e., < 4 cm, 4–8 cm, 8–12 cm and > 12 cm) (Fig. 2). All detailed studies on various aspects of drilling predation, including predator-prey behavioural data (e.g., size and site selectivity), were only made for the three abundant Indian species ($n = 1,106$). Otherwise, all samples were pooled together to identify spatial trends at global scale.

The majority of drill holes on the studied turritelline species are “truncated spherical paraboloids”, which are typical of those made by naticid gastropods (Carriker & Yochelson, 1968; Carriker, 1981). Drilling frequency has been calculated as percentage of shells with at least one complete drill hole divided by the total number of shells (N) (Allmon et al., 1990). Unsuccessful and multiple drill holes speak for prey effectiveness against predation. Frequency of unsuccessful drill holes has been defined as a ratio between total incomplete drill holes and total number of attempted holes, while frequency of multiple drill holes has been defined as number of drill holes which are found in multiple drilled specimens divided by the total number of attempted holes (Vermeij, 1987; Kelley et al., 2001). For peeling

predation, we have concentrated on repaired peeling scars only. Predators can attack turritelline gastropods in different ways: some of them will break the spire, some completely crush the shell, and some ingest the prey whole (Allmon, 2011). These activities are almost impossible to track in dead turritelline shells. In comparison, unsuccessful apertural peeling by calappid crabs, as indicated by repair scars, is relatively convenient to trace and quantify. Aperture-parallel repair scars, which represent minor lip breakage, have been excluded from the quantification of peeling predation (Vermeij & Dudley, 1982), as these types of breaks can also be caused by physical agents. PF has been calculated as the total number of repair scars divided by the total number of shells examined, expressed in decimal values (Allmon et al., 1990).

In order to understand predator behaviour (i.e., size- and site-selectivity), the following observations have been made: relationship between outer bore hole diameter (OBD, which tells about size of the predator involved; Kitchell et al., 1986) and prey size (plot of OBD against prey length); and vertical and radial positions of the drill holes with respect to shell base and apertural plane, and also the location of holes on the whorl. Our null hypothesis was that the drill holes are distributed randomly, both vertically and radially. Prey size was measured in two different ways: length from apex to the base of aperture (L), and the maximum whorl diameter (D), measured at last whorl.

Previous studies on turritellines have attempted to address how specific prey adaptations can influence predation (Signor, 1985; Allmon et al., 1990; Tull & Bohning-Gaese, 1993). In general, it would be expected that robust and ornamented forms are relatively more resistant than less sculptured forms. Allmon et al. (1990) used a qualitative measure of shell ornamentation to rank them in different defensive categories. We have developed a similar, more quantitative rather than qualitative ornamentation scheme, based on strength and number of ribs present on these species (Table 2). Based on it, we have put all turritelline species into four different ornamentation classes. If a species has only weak ribs, we have counted the number of these weak ribs to classify them into different ornamentation classes. For example, category 1 has no strong ribs; it has less than/equal to five weak ribs. Any species which have only one strong rib or five to eight weak ribs will be ranked as category 2. This scheme

TABLE 2. Classification of different turritelline species of Indian subcontinent based on their strength of ornamentation. Relationship between predation frequencies (DF and PF) with ornamentation index is also shown. See text for details.

Ornamentation Index	Number of strong ribs	Number of weak ribs	N	DF	PF
Class 1	0	≤ 5	4	25%	2.5
Class 2	1	5-8	801	15.23%	2.07
Class 3	2	1–2	307	14.66%	0.94
Class 4	> 2	> 3	154	10.39%	0.73

gives maximum weighting to number of strong ribs and then number of weak ribs present on shells. Shell slenderness (i.e., high L to D ratio) also appears to influence predation, either because slender species are difficult to detect and capture (Allmon et al., 1990), or because their smaller aperture size discourages peeling predators (Signor, 1985). In addition, we have measured shell thickness (T) in two ways. Firstly, at different growth stages (by breaking the shell), to document ontogenetic variation; secondly, at the apertural margin.

Because most of the specimens considered here were likely collected dead, taphonomic processes may have biased the samples; drilled shell may behave differently during transportation and may be preferentially broken (Dudley & Vermeij, 1978; Roy et al., 1994; but see Hagstrom, 1996; Kaplan & Baumiller, 2000; Zuschin & Stanton, 2001). On the other hand, drilled shells may be better preserved because a naticid takes its prey within the sediment before drilling (Edwards, 1974). Hermit crabs can also alter general trends of taphonomic preservation of shells since they accept both infaunal and epifaunal gastropod shells. Because of these complexities, we have assumed that the drilled and undrilled shells have equal preservation potential, following others (Dudley & Vermeij, 1978; Vermeij & Dudley, 1982; Allmon et al., 1990; Tull & Bohning-Gaese, 1993; Hagadorn & Boyajian, 1997).

RESULTS

Predation on Indian Subcontinental Species

Drilling Predation

Drilling Frequency: Among the three most abundant Indian species, *T. attenuata* shows

the highest value of DF (15.23%, n = 801), which is not significantly different from *T. duplicata* (13.47%, n = 230, p = 0.5081). In contrast, DF on *T. acutangula* is very low (6.67%, n = 75) (Table 1). Ontogenetic variation in DF is also evident in all three species; smaller individuals (< 4 cm in length) show higher DF and it decreases as the prey body size increases (Table 1, Fig. 2).

Data from ZSI and our collections, representing 14 turritelline species from the Indian subcontinent, show overall DF of 14.24% (n = 1,222). Ontogenetic variation in DF is not evident, smaller individuals (< 4 cm) show DF of 16.36% (n = 324), which is comparable with DF for larger counterpart (> 4 cm) 13.47% (n = 898; p = 0.2019) (Table 1).

Frequencies of incomplete drill holes also show insignificant variability. For *T. attenuata*, *T. duplicata* and *T. acutangula*, the values are 2.58%, 2.17%, and 3.08% respectively. Multiple drill holes are rare for *T. duplicata* (0.65%) and *T. attenuata* (0.25%); no instance of multiple drill holes has been found in *T. acutangula*.

Within-species spatial variations in DF for turritellines are also evident. For example, *T. attenuata* in Digha (21°41'N, 87°33'E) shows overall drilling frequency of 12.16% (n = 329), while in Chandipur (21°28'N, 87°01'E) it is 18.83% (n = 430) (p = 0.0129). Similarly, for *T. duplicata*, drilling frequency varies from 9.8% (n = 51) at Baluchisthan (28°53'N, 64°25'E) to 28.57% (n = 42) at Dwarka (22°14'N, 68°58'E) (Table 1) (p = 0.0198).

Predator Behaviour: When size stereotypy of predation was studied by plotting predator's size (i.e., OBD) against prey shell length, *T. attenuata* shows overall poor correlation (r² = 0.003, p << 0.005) (Fig. 3A), but the sample from Digha shows relatively good correlation (r² = 0.285). In the case of *T. duplicata*, this relation

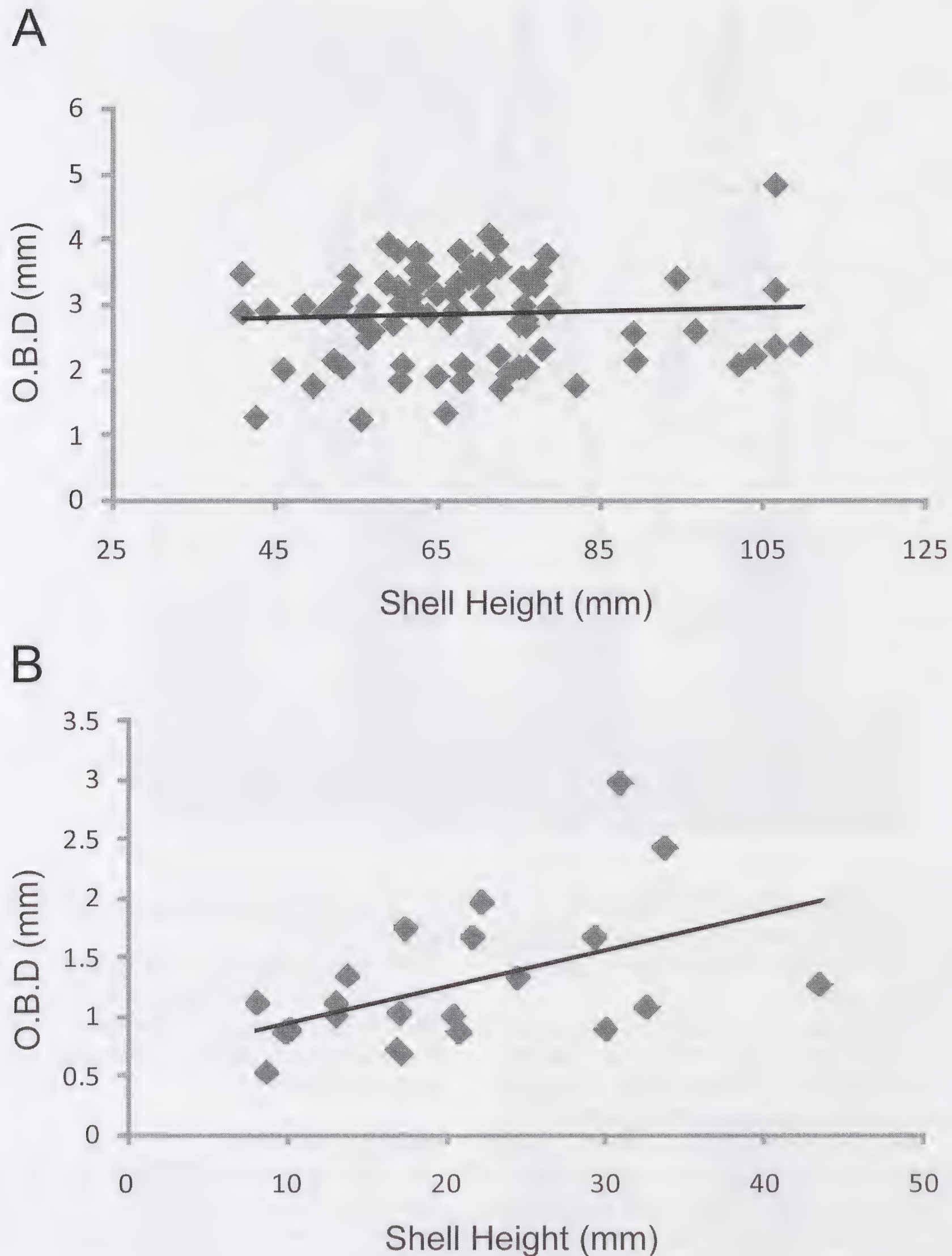


FIG. 3. Relationship between outer borehole diameter (OBD, proxy for predator size) of naticid drill holes and prey shell height for *T. attenuata* (3A); $y = 0.002x + 2.579$ (n = 87, $r^2 = 0.003$, $p = 7.791E-22$) and *T. duplicata* (3B); $y = 0.030x + 0.630$ (n = 22, $r^2 = 0.238$, $p = 1.433E-08$).

holds true ($r^2 = 0.238$, $p = 0.0115$) (Fig. 3B). We do not have enough samples for *T. acutangula* to show such correlation.

Predator site selectivity for drilling was studied by looking at distributions of drill holes on the prey shell, both vertically and radially. In vertical profile, drill holes are highly stereo-

typed; that is, mostly located on the last two whorls away from the aperture in *T. attenuata*, while, for *T. duplicata*, holes are randomly (no preferential site) distributed throughout the shell (Fig. 4). In a radial quadrant system, drill holes on both *T. attenuata* and *T. duplicata* are equally distributed in both apertural (I and

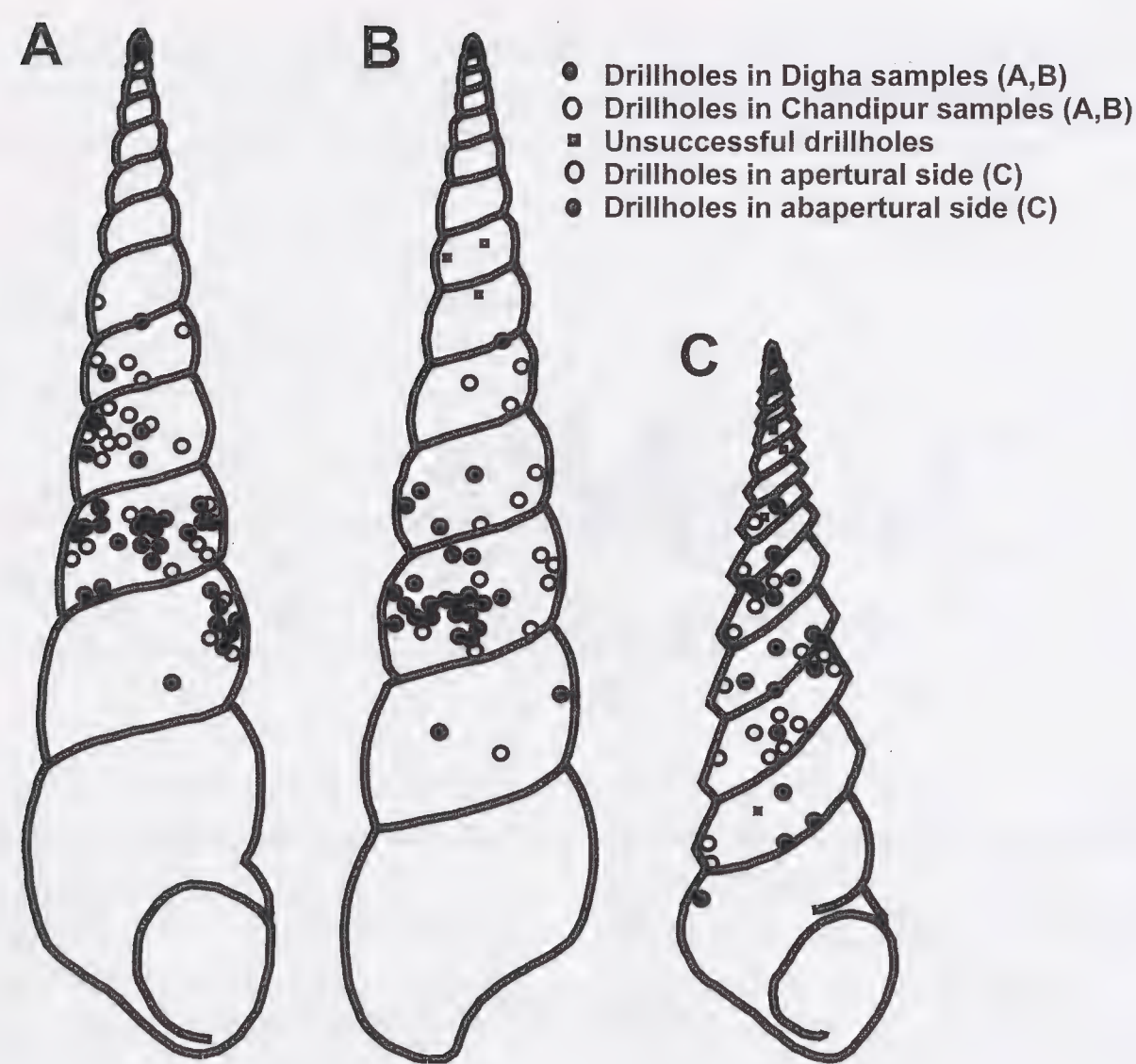


FIG. 4. Schematic diagrams showing vertical position of drill holes on apertural (A) and abapertural (B) sides of *T. attenuata* (n = 103) from different localities. For *T. duplicata* (n = 40) apertural and abapertural drill holes are represented in a single figure (C). Symbols in the inset provide drill hole information for different sides.

IV) and abapertural (II and III) sides (Fig. 5). *T. acutangula* has low drilling frequency (only five shells are drilled) and therefore the stereotype has not been studied.

Drill hole (both successful and unsuccessful) positions on the whorl (360° segment of a helically coiled shell) were studied to see whether they were located on the suture or whorl (Fig. 4). For *T. attenuata*, 77.5% of successful holes were located near the mid-whorl and 22.5% were located on the suture or close to it. Similarly, for *T. duplicata*, 71.8% successful holes were located near the mid-whorl, and 28.2% were located near or at the suture. Unsuccessful holes are more common on *T. attenuata*, with 66.67% located on the whorl. The majority (72.22%) of unsuccessful holes, however, are located beyond the stereotyped area (where most of the successful holes are located), that is, towards the apex. In *T. duplicata*, unsuccessful drill holes (n = 5) are found on the whorl as well as on the suture.

Anti-Drilling Prey Features: For *T. attenuata* and *T. acutangula*, shell thickness increases with ontogeny (Fig. 6, $r^2 = 0.7044$ and 0.8529 , respectively). In *T. duplicata*, shell thickness (r^2

$= 0.0052$) does not change significantly during growth (Fig. 6).

The three species were categorized on the strength of ornamentation (Table 2): *T. attenuata* belongs to class 2, whereas *T. duplicata* and *T. acutangula* have been classified into class 3 and 4 respectively.

Peeling Predation

Peeling Frequency: PF is highly variable, from species to species, as well as with ontogeny within a species. *Turritella attenuata* shows a maximum PF of 2.07 (n = 801), while two other species show relatively low frequencies of peeling (0.81 for *T. acutangula* and 0.9 for *T. duplicata*) (Table 1).

The overall PF from the Indian subcontinent, incorporating all 14 species together, shows a value of 1.62 (n = 1,222). Smaller specimens (< 4 cm) have a lower PF (0.5, n = 324), compared to the larger shells (2.02, n = 898) (Table 1). This type of size dependence is also evident for the three most abundant species.

Peeling frequency for a single species also varies spatially (Table 1). For example, *T. attenuata* from Chandipur shows PF of 1.61 (n =

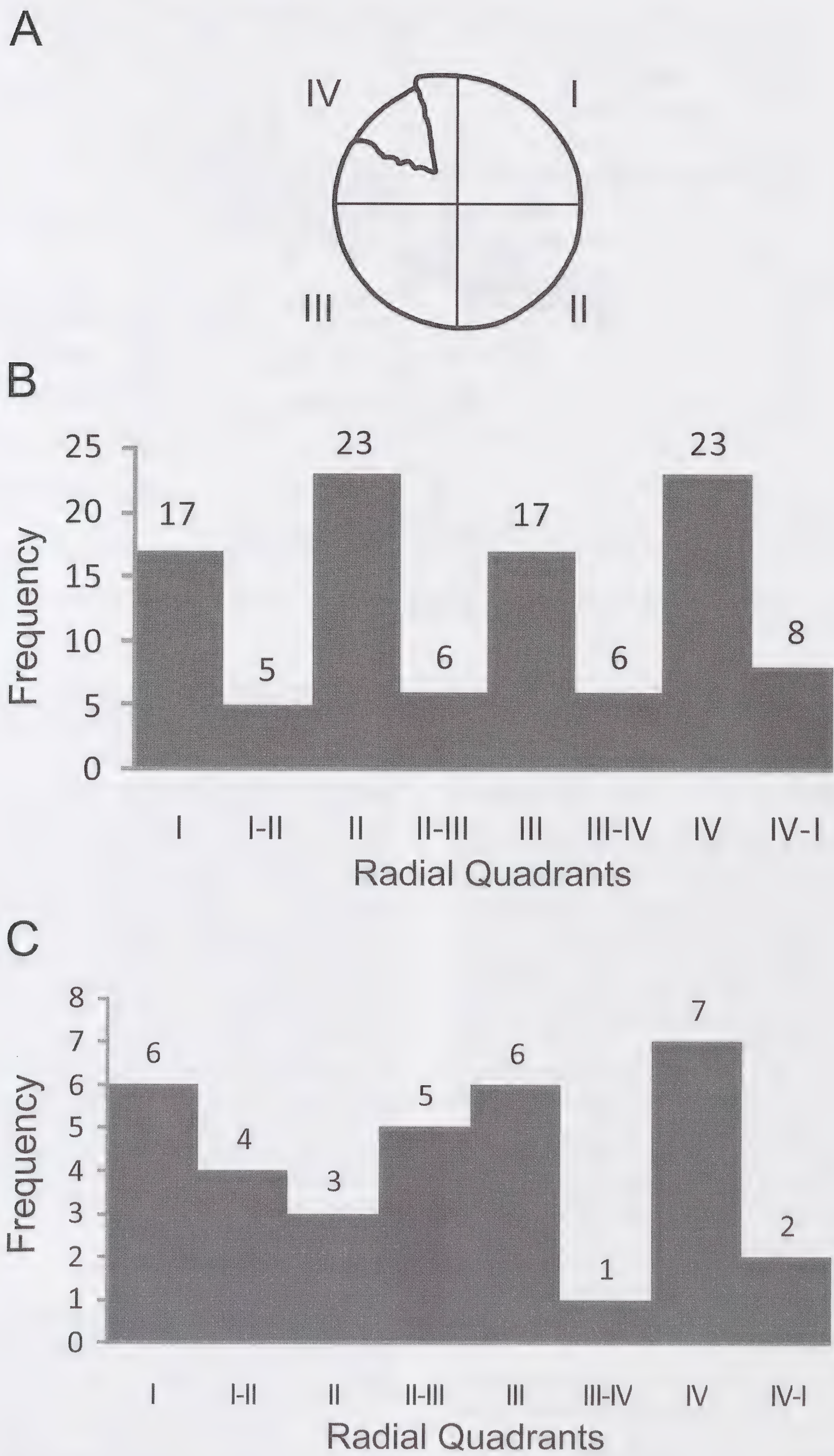


FIG. 5. A) shows the base of a turrnelline shell indicating the distribution of different quadrants in radial system (after Allmon et al., 1990), B) and C) show radial distribution of drill holes on intact shells of *T. attenuata* (n = 105) and *T. duplicata* (n = 34) respectively.

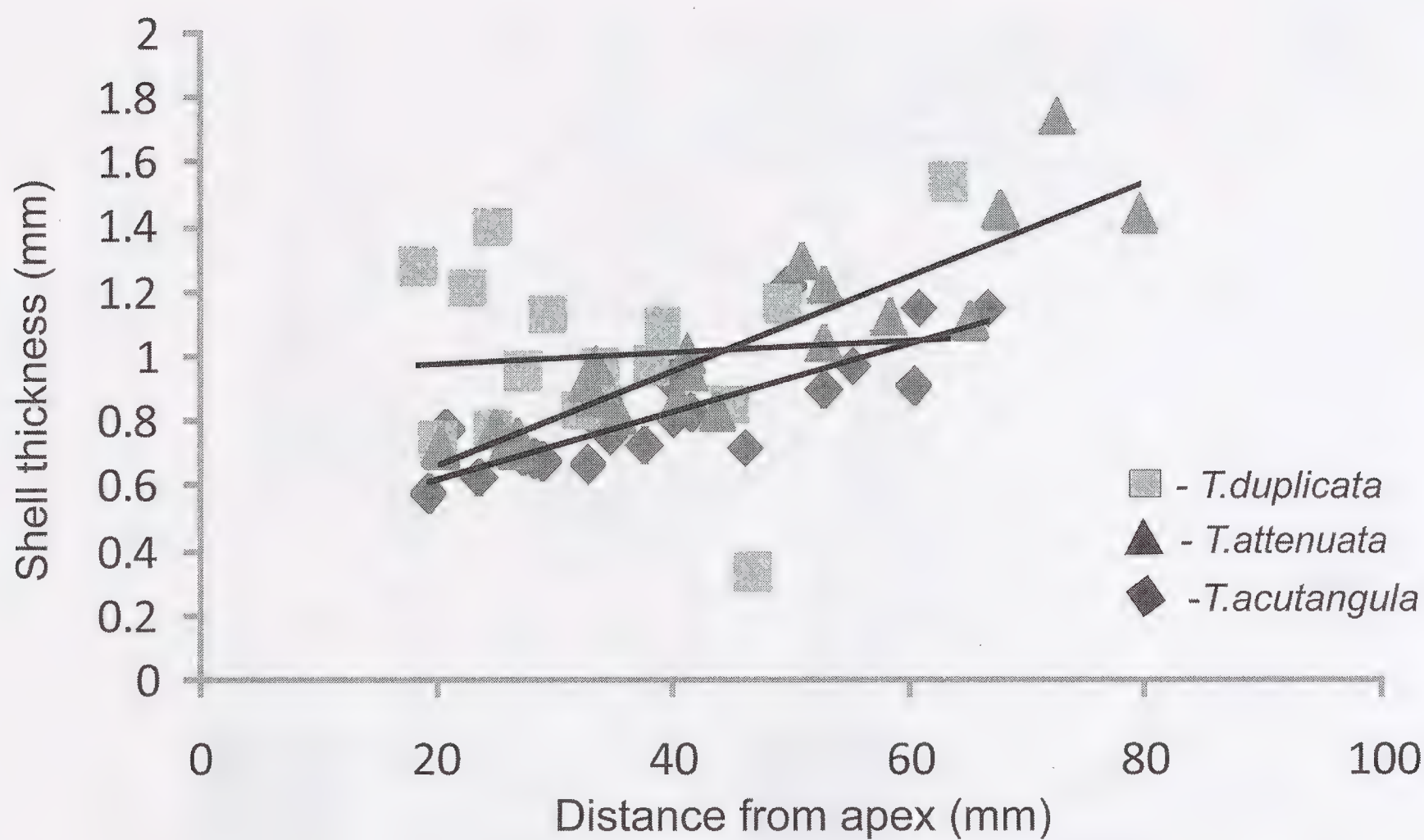


FIG. 6. Variation of shell thickness at different distances from the apex of the three abundant Indian species.

430), while samples from Digba show a value as high as 2.57 (n = 329) (p = 0.0011). Similarly, for *T. duplicata*, PF varies from 0.37 (n = 51) in Baluchistan to 0.76 (n = 42) at Dwarka (p = 0.0002).

Anti-Peeling Prey Features: Recent turritelline species show wide interspecific diversity of shell geometry (Allmon, 2011). Slenderness (ratio of shell diameter, D, to shell length, L) can be used to group them into different categories. Even at a similar size, some species are more slender (e.g. *T. columnaris*; D/L = 0.22), and others are inflated (e.g., *T. duplicata*; D/L = 0.39). It is seen that PF decreases with an increase in D/L values i.e., inflated species are more resistant to peeling (Fig. 7).

Mean shell thickness at the aperture, normalized by maximum whorl diameter, for the three abundant Indian species does not vary signifi-

cantly (p = 0.5) (Table 3), but PF varies significantly among them. This suggests that greater shell thickness at the aperture is not effective against peeling predation. The persistence of a thin shell at the aperture may be a result of morphological constraint (Seilacher, 1970; Gould, 1980). It indicates that, thin aperture in turritellines is inherited from ancestors and a symplesiomorphic character of the family (see also Marwick & Hutt, 1957). But ornamental strength (definition: Table 2) varies greatly within turritelline species and has a negative correlation with peeling intensity. According to our ornamentation scheme, *T. attenuata* belongs to class 2 and has an overall peeling frequency of 2.07 (n = 801), whereas *T. duplicata* (class 3) and *T. acutangula* (class 4) have overall peeling frequencies of 0.9 (n = 230) and 0.81 (n = 75) respectively (p = 0.0387) (Table 2).

TABLE 3. Mean apertural thickness, normalized by maximum whorl diameter (MWD), of the three abundant Indian species.

Species	Mean apertural thickness / MWD
<i>T. attenuata</i>	0.0272
<i>T. duplicata</i>	0.0307
<i>T. acutangula</i>	0.0237

Global Predation Trends

Recent turritelline species are diverse and distributed globally (Allmon, 2011). We combined data from the literature and the collections discussed here to make a new global dataset to track the global trends of naticid predation and crab peeling on turritelline gastropods. The analyses of these data reveal that overall DF of all Recent turritellines is 32.55% (n = 5,950; Buchanan, 1958; Dudley & Vermeij, 1978; Tull

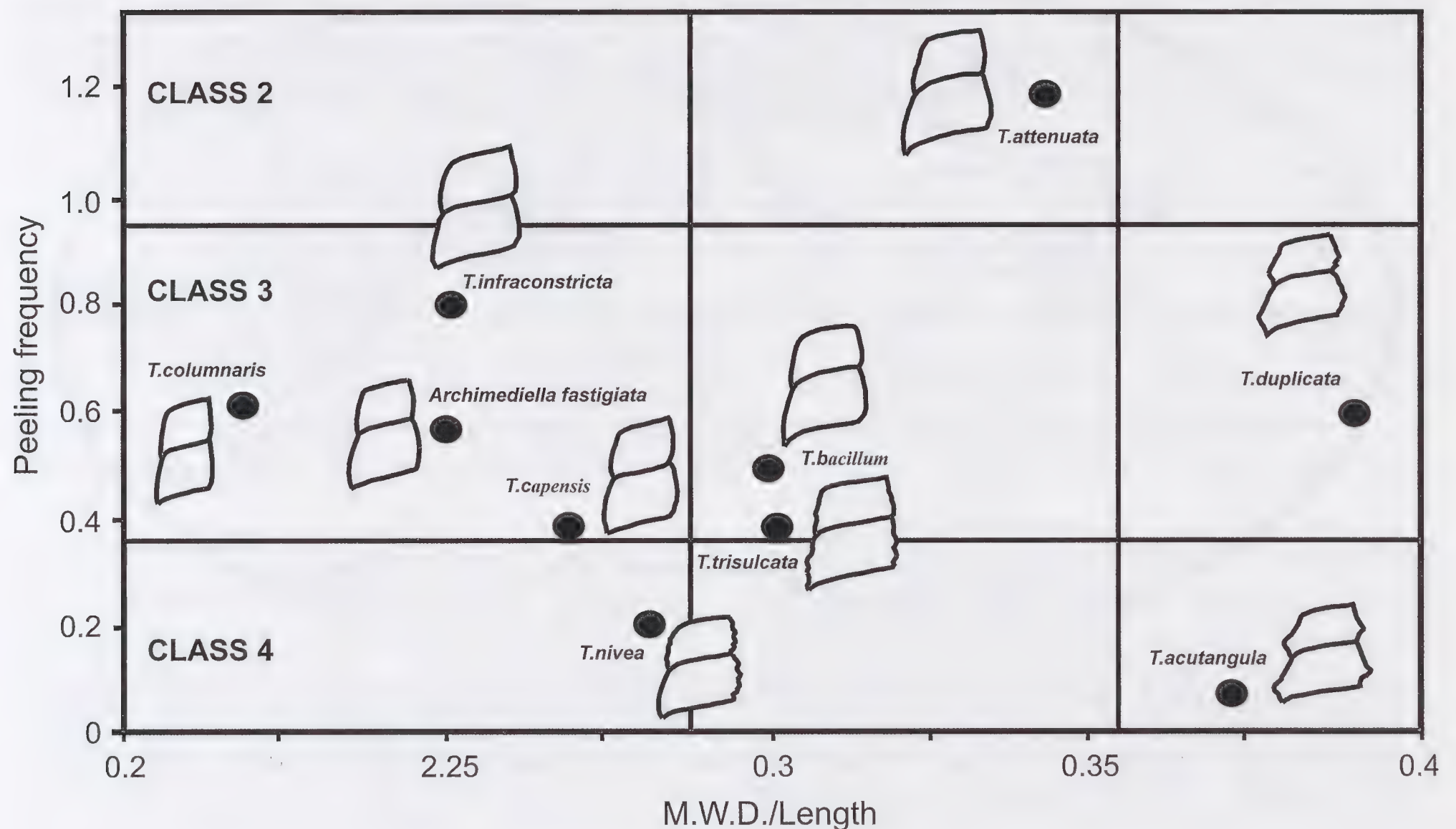


FIG. 7. Relationship among peeling frequency (PF), shell geometry and ornamental strength (subjectively ranked into different classes; for details see text).

& Bohning-Gaese, 1993; Sawyer & Zuschin, 2010; present data), and overall PF is 1.47 ($n = 1,561$; Gerhard et al., 1997; present data). For detail, see Appendix 1. Drilling and peeling frequencies vary in different size classes. Larger specimens (> 4 cm) show drilling and peeling frequencies of 18.43% ($n = 1,595$) and 2.09 ($n = 945$), respectively, whereas smaller specimens (< 4 cm) show 22.18% ($n = 1,709$) and 0.54 ($n = 508$), respectively (Dudley & Vermeij, 1978; Tull & Bohning-Gaese, 1993, Gerhard et al., 1997; present data). We have excluded some references from this analysis because of the lack of size data (e.g., Buchanan, 1958; Sawyer & Zuschin, 2010).

DISCUSSION

The new data presented here, along with other recent literature (Dudley & Vermeij, 1978; Allmon et al., 1990; Tull & Bohning-Gaese, 1993; Hagadorn & Boyajian, 1997), has prompted us to expand the documentation, analysis and interpretation of drilling and peeling predation on Recent turrilline gastropods throughout the world.

Allmon et al. (1990) stated that functional analyses of turrilline shells are difficult and

challenging. Some of the species have active defensive responses (Allmon, 2011), and some show behavioral avoidance of predators (Allmon et al., 1990). Predator-prey interaction can also be underestimated or overestimated due to such other biotic factors as predator availability, prey avoidance, prey preference, and diversity and the abundance of both predators and prey. The nature of naticid predation such as multiple strategies against prey (e.g., killing a prey species either by drilling or by smothering, as observed in several species of the genus *Polinices*; Vermeij, 1980; Ansell & Morton, 1985, 1987, Kabat, 1990) and fish predation by either crushing or swallowing (Dudley & Vermeij, 1978; Zipser & Vermeij, 1978) may also affect the nature of the record of predation. Our very large sample size reveals some interesting aspects of turrilline predation which will be discussed here.

Drilling Predation

Drilling Frequency

The average drilling frequency on all Recent turrilline gastropods from the Indian subcontinent is 14.24% ($n = 1,222$) which is not significantly different from the DF when only the three most abundant Indian species

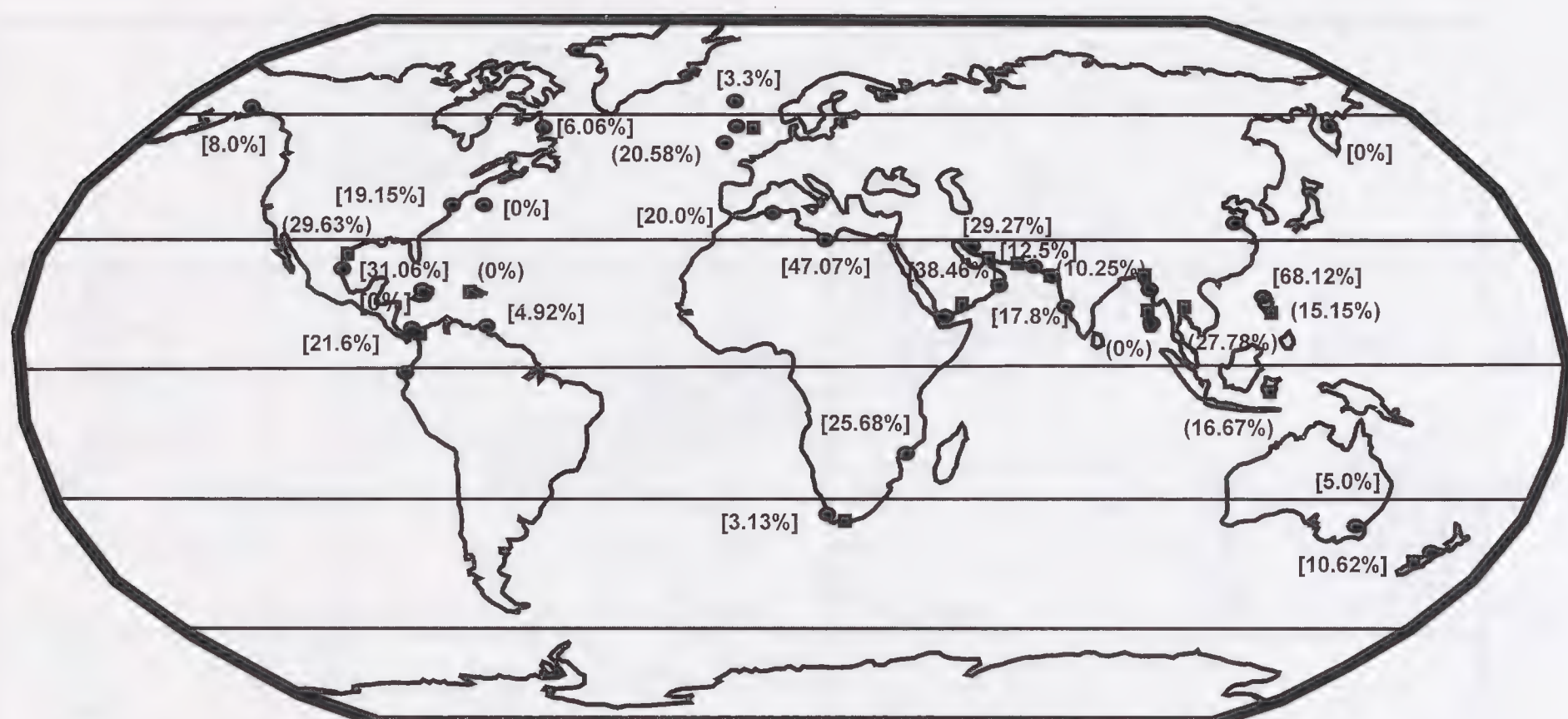


FIG. 8. Geographic distribution of drilling predation on turritelline gastropods. Circles represent smaller samples and squares represent larger samples. Drilling percentages for localities having specimen numbers more than 10 are enclosed within square brackets, smaller samples in parentheses. For the rest only symbols are plotted.

(14.69%, $n = 1,137$; $p = 0.7561$) were considered. Both values are low with respect to the DF for all turritelline gastropods worldwide, which is 32.55% ($n = 5,950$; $p < 0.0001$). One conspicuous trend in predation on turritelline gastropods is that predation frequency varies with prey size classes (Dudley & Vermeij, 1978). For drilling predation, DF decreases with increase in prey shell size for each of the three most abundant Indian species (18.18% for shells below 4 cm and 13.24% for shells above 4 cm; see Table 1). Even further subdivision of size distribution (e.g. < 4 cm, 4–8 cm, 8–12 cm, and > 12 cm) shows the same trend (Fig. 2). Drilling frequencies drop drastically above 4 cm. Smaller individuals (< 4 cm) of all Indian subcontinental species show relatively higher drilling frequency (16.36%) compared to the larger size class (13.47%) (Table 1; Tull & Bohning-Gaese, 1993). This observation is consistent with the idea that larger individuals are relatively more resistant against drilling predation (Dudley & Vermeij, 1978; Allmon et al., 1990; Tull & Bohning-Gaese, 1993). Within the Indian subcontinent, out of the 14 species studied, only three species (21%) have adult body sizes smaller than 4 cm. It may explain why the Indian population shows a relatively low drilling frequency compared to the rest of the world, of which, out of 31 species (whose drilling data are known; Table 1; Dudley & Vermeij, 1978), 19 species (61%) are smaller than 4 cm.

A higher DF in smaller specimens is also evident in previous studies of the fossil record (Dudley & Vermeij, 1978; Arua & Haque, 1989; Allmon et al., 1990; Tull & Bohning-Gaese, 1993; Hagadorn & Boyajian, 1997). The higher drilling frequency in smaller specimens may be due to several reasons; naticids may target young individuals for easy manipulation of prey, or it may simply be a change in the life mode of the prey during ontogeny. Waite & Strasser (2011) suggested that the smaller individuals of *T. duplicata* (mainly below 4 cm length) may live infaunally, while the larger individuals may be more frequently on top of the sediment surface; this might result in more predation on juveniles since naticid predators generally target infaunal prey (Sawyer & Zuschin, 2010).

Despite having the same shell morphology and size classes, some individual species show geographic variation in DF. Drilling frequency also varies for different species from different areas (Allmon et al., 1990). Among the three abundant Indian species, *T. attenuata* shows significant variation within the different areas of the eastern coast. The Digha population has drilling frequency of 12.16% ($n = 329$) while the Chandipur population occurring about 80 km south has 18.83% DF ($n = 430$; $p = 0.0129$). One possible reason may be that naticid are both abundant and diverse in Chandipur (Subba Rao et al., 1991) and frequently drill other prey taxa (Mondal et al., 2010). But if different populations of the same species are

TABLE 4. Latitudinal variation of predation frequencies (DF and PF) based on global database. Numbers within parentheses indicate specimen numbers. See text for details. Note that data for PF from 60°–70° are not available. Sources: Buchanan, 1958; Dudley & Vermeij, 1978; Tull & Bohning-Gaese, 1993; Gerhard et al., 1997; Sawyer & Zuschin, 2010; present data.

Predation frequencies	Latitudes						
	0°–10°	10°–20°	20°–30°	30°–40°	40°–50°	50°–60°	60°–70°
DF	55.7% (521)	22.3% (2,103)	22.3% (341)	12.8% (390)	10.1% (119)	0% (28)	6.7% (105)
PF	3.21 (14)	1.85 (985)	0.59 (118)	0.83 (210)	1.58 (12)	2.83 (8)	-

geographically widespread, they may show more latitudinal variation. For *T. duplicata*, drilling frequency varies from 9.8% (n = 51) at Baluchistan to 28.57% (n = 42; p = 0.0198) at Dwarka, which is about 2,358 km south of the former and is closer to the subtropics. Similar latitudinal differences may be seen when the global data are pooled for the all Recent turritelline species (Fig. 8, Table 4).

Predator Behavior

The behavior of predators is important to understand the dynamics of predator-prey interaction. Numerous studies of naticid gastropods have revealed that their predatory behaviour has evolved with time. Prey handling, prey manipulation, drilling site selection, prey preference, etc. have become more efficient (Vermeij, 1983; Kelley & Hansen, 1993, 1996; Dietl & Alexander, 2000). The new data set discussed here may allow investigation of these parameters.

Preference of vertical location for drilling reflects predator’s efficiency to drill on the thinnest part of the shell (Kitchell, 1986). *Turritella attenuata* shows stereotyped site selection. Most of the drill holes are concentrated at 50%–60% of the shell length from the apex, that is, two whorls away from the aperture (Fig. 4). Allmon et al. (1990) and Hagadorn & Boyajian (1997) also found similar site selectivity in fossil turritelline species. Allmon et al. (1990) argued that this site preference is related to predator’s behaviour of choosing the thinnest part of the shell, but did not provide any quantification for thickness. Among the three abundant species, we did not find any support for this generalization. For two species (*T. attenuata* and *T. acutangula*), shell thickness is positively correlated with ontogeny (Fig. 6), and it appears that the preferred site is not the thinnest part of the shell. This observation is not consistent with the prediction of the general cost-benefit theory

(Kitchell, 1986) and needs further attention. In *T. duplicata*, shell thickness does not change significantly during ontogeny which may explain the lack of drill hole site stereotypy (Fig. 6).

Radial location of drill holes is another measure of predatory selectivity because it indicates whether the naticids attempt to drill into the apertural or abapertural side of the prey shell (Adegoke & Tevesz, 1974). For turritellines, quadrants II and III (Fig. 5) will be mostly targeted when the prey crawls above the sediment. Quadrant I and II will be targeted when the prey is stationary in its infaunal live position (Allmon, 2011; Waite & Strasser, 2011). If this generalization is true, then turritellines would be expected to have most drill holes at site II (the most common vulnerable site during both crawling and sedentary life modes). Allmon et al. (1990) showed preference for abapertural quadrants in fossil turritellines, but we found no such preference for a particular quadrant (Fig. 5; Hagadorn & Boyajian, 1997). This suggests that there may be significant species-specific variation in this aspect of site selection, perhaps related to the prey’s escape behaviour (Kabat & Kohn, 1986), or that individuals of the same species may sometimes remain infaunal and sometimes crawl over the substrate (Waite & Strasser, 2011).

Correlation between predator size and prey size is another important criterion for evaluating size selectivity by predators. In *T. attenuata*, the overall correlation is poor (Fig. 3A), but the sample from Digha shows better results. This is mainly because naticid diversity and abundance are less in Digha, mostly dominated by *Polinices didyma* (Röding, 1798) and *Natica tigrina* (Röding, 1798), whereas in Chandipur naticid diversity and abundance are very high (Subba Rao et al., 1991) and adult size of the predators range from 1.4 cm (*Eunaticina* sp.) to 5.2 cm (*Polinices didyma*). It may be that mul-

tiple naticid species may attack *T. attenuata*, and such multispecies predation may blur the correlation between a specific predator and its prey. *Turritella duplicata* whereas shows relatively good correlation between outer borehole diameter (OBD) and prey size (Fig. 3B).

Anti-Drilling Prey Features

It appears that the less ornamented *T. attenuata* shows the maximum DF, whereas the more strongly sculptured *T. acutangula* has the lowest value. This pattern is true for both smaller and larger individuals (Table 1). For all 14 Indian species, a relation also exists between DF and the strength of the ornamentation. DF decreases with increasing ornamental index (Table 2) as well as size (Table 1).

Dudley & Vermeij (1978) demonstrated that ornamentation in turritelline species provides resistance to drilling. Strongly ornamented forms are less frequently preyed upon. Allmon et al., (1990) supported this general trend, but mentioned that this is not consistent when only the most ornamented forms are studied. Our results do not support the observation made by Allmon et al. (1990). For the turritellines of the Indian sub-continent, the species having relatively weaker ornamentation show higher drilling frequency while the stronger sculpture show low drilling intensity (Table 2). This trend holds good for all size classes. Out of 13 Indian species, eight of them (61.54%) belong to strongly ornamented classes (see Table 2). The biogeography of ornamented species of Indian turritellines shows a distinct pattern. The more strongly ornamented species (class 4), for example *T. acutangula*, live in the open marine southern coast of Indian peninsula. *Turritella attenuata*, which is more weakly ornamented, lives in restricted bays on the eastern coast (Fig. 1). The other, more strongly ornamented species are found mostly in the more highly agitated waters of the Andaman Islands (Subba Rao & Dey, 2000). It is a common observation that strength and the number of ribs in bivalve genera (e.g., *Anadara* and *Cardium*) increase in high energy environments (Stanton & Dodd, 1970; Alexander, 1974). Strong spiral ornamentation in turritellines may resist drilling predation, but is less effective against peeling predation. Axial ridges are better resistant to shell breakage (Vermeij, 1982). Spiral ribbing characterises the entire subfamily Turritellinae (Marwick & Hutt, 1957), and turritellines may therefore be phylogenetically constrained (cf., Seilacher, 1970), preventing them from evolving axial ornamentation.

Peeling Predation

Peeling Frequency

The average PF on Recent turritelline gastropods from Indian subcontinent is 1.62 (n = 898). This PF is comparable to that of all turritelline gastropods worldwide, which is 1.47 (n = 1561) (p = 0.7701). The general trend of peeling predation in turritelline gastropods for both the Indian subcontinent and the world is that predation frequency varies with prey size class. Smaller individuals, less than 4cm in length, show lower peeling frequency (0.5) compared to the larger size class (2.02) (see Table 1). Allmon et al. (1990) also made similar observations for fossil turritelline gastropods (Miller, 1975; Zipser & Vermeij, 1978; Vermeij, 1982; Vermeij & Dudley, 1982; but see Kabat & Kohn, 1986). Vermeij et al. (1980) reasoned that the larger shell is likely to have sustained more non-lethal attacks. The low PF in young specimens of larger species or adult specimens of smaller species may be due to the fact that they live predominantly infaunally (Waite & Strasser, 2011) and may thus escape the notice of epifaunal crabs (Campbell & Fielder, 1986).

Anti-Peeling Prey Features

In case of high spired forms, PF may vary with shell geometry (Zipser & Vermeij, 1978; Vermeij, 1981; Signor, 1985). In recent terebrid species, inflated forms show a higher incidence of repair scars than slender species (Signor, 1985). Allmon et al. (1990), however, did not find such a correlation in turritelline fossil assemblages since the Cretaceous, and our analysis is consistent with their results (Fig. 7). Both slender and inflated forms suffer a wide range of PF values. Within slender species there is no particular trend of decreasing PF with the increase in degree of inflation. Instead, a good correlation between ornamental strength and peeling frequency reveals specific prey adaptation against peeling (Vermeij, 1981). Highly ornamented forms (class 3 and 4) have a lower value of peeling frequency than weakly ribbed species (class 1 and 2, p << 0.01, chi-square test of independence: see also Fig. 7). Two species, however, show anomalous positions contrary to our expectations. The position of *T. bacillum* (n = 2; class 1) and *T. infraconstricta* (n = 5; class 4) may be due to low sample size.

Strongly ornamented shells might be expected to have lower values of peeling frequencies (Allmon, 1990). Perhaps the pattern in turritellines is due to the style of the ornamentation. Ornaments in terebrid gastropods are mainly

axial and the outer lip of the aperture is thick. These features resist shell breakage due to peeling. But in case of turritelline gastropods the outer lip is always thin and ornaments are spiral and these make the shell less effective against peeling predation. If any breakage occurs it will therefore penetrate further into the whorl than in terebrids. Paleozoic ammonoids may provide an analogous case. Many genera of ammonoids during Palaeozoic were spirally ribbed, but during the Mesozoic, the ribbing became mostly radial, which would perhaps align breakage parallel to the peristome margin and cause less damage to the whorl. For this reason, the evolution of radial ribs in ammonoids has been explained as the development of breakage-resistant features against the injuries mainly caused by decapod crustaceans (Ward & Wicksten, 1980; Ward, 1981).

Spatial Variability

Latitudinal variation in predation frequencies is evident for turritelline gastropods (Table 4). There is a steady decrease of DF, from 55.7% in low latitude (0° – 10°) areas to 6.7% in high latitude areas (60° – 70°), except the areas lying within the (50° – 60°) latitudinal bin, which records 0%. This may be due to the small number of specimens ($n = 28$) from this area. Previously, Dudley & Vermeij (1978) also estimated the latitudinal variation of DF and our expanded data supports their results.

The PF in Recent turritellines shows a broad latitudinal trend. Tropical, or near tropical (0° – 20°) species show higher incidences of PF (3.21 to 1.85) than their temporal (20° – 40°) counterparts (0.59 to 0.83), but PF again increases (1.58 to 2.83) in higher (40° to 60°) latitudinal bin (Table 4). This may be due to low sample size ($n = 20$). Similar latitudinal trends have been also observed in terebrid and other gastropods (e.g., thaidids and littorinids; Vermeij, 1982, and references therein).

CONCLUSIONS

(1) Drilling and peeling frequencies in Recent turritellines vary spatially; frequencies of predation decrease towards higher latitudes. Pooled frequencies of predation may therefore be of limited utility for testing specific evolutionary-ecological hypotheses, even in a taxon-level study.

(2) In general, smaller individuals show higher drilling and lower peeling frequencies. When all species are pooled together, this relation

becomes blurred for drilling predation. These patterns are consistent with the hypothesis that shell ornamentation is an anti-drilling trait in turritellines but less effective against peeling predation.

(3) Size-selectivity is widely variable both intraspecifically and interspecifically. For this reason, size selectivity may not be useful in testing hypotheses of escalation in this group.

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APPENDIX 1. New global dataset of drilling and peeling predation on Recent turritelline gastropods.

Family Turritellidae	n	No of drill holes	No of repear scar	DF (%)	PF	Authors
<i>T. attenuata</i>	815	97	1,973	12%	2.42	Present Data
<i>T. duplicata</i>	193	32	173	17%	0.9	Present Data
<i>T. acutangula</i>	65	3	56	5%	0.86	Present Data
<i>T. bacillum</i>	2	1	0	0%	0.5	Present Data
<i>T. terebra</i>	5	20	0	0%	4	Present Data
<i>T. columnaris</i>	47	10	65	21%	1.38	Present Data
<i>T. trisulcata</i>	39	8	20	21%	0.51	Present Data
<i>T. nebulosa</i>	1	1	0	100%	0	Present Data
<i>T. capensis</i>	20	2	7	10%	0.35	Present Data
<i>T. fascialis</i>	26	10	3	38%	0.16	Present Data
<i>T. vitullata</i>	17	1	14	6%	0.82	Present Data
<i>T. sinuata</i>	14	4	11	29%	0.79	Present Data
<i>T. carinifera</i>	17	1	26	6%	1.53	Present Data
<i>T. nivea</i>	30	3	7	10%	0.23	Present Data
<i>T. fastigiata</i>	9	2	7	22%	0.78	Present Data
<i>T. infraconstricta</i>	6	0	5	0%	0.83	Present Data
<i>T. monilifera</i>	1	0	3	0%	3	Present Data
<i>T. rosea</i>	12	0	19	0%	1.58	Present Data
<i>T. variegatus</i>	5	0	18	0%	3.6	Present Data
<i>T. fuscocincta</i>	31	0	8	0%	0.26	Present Data
<i>T. hanleyana</i>	1	0	9	0%	9	Present Data
<i>T. cornea</i>	8	0	22	0%	2.75	Present Data
<i>T. exolata</i>	18	0	9	0%	0.5	Present Data
<i>T. maculata</i>	8	3	13	38%	1.63	Present Data
<i>T. erosa</i>	28	4	-	14.3%	-	Dudley & Vermeij, 1978
<i>T. erosa</i>	70	6	-	8.6%	-	Dudley & Vermeij, 1978
<i>T. erosa</i>	11	0	-	0%	-	Dudley & Vermeij, 1978
<i>T. erosa</i>	48	5	-	10.4%	-	Dudley & Vermeij, 1978
<i>T. reticulata</i>	29	0	-	0%	-	Dudley & Vermeij, 1978
<i>T. reticulata</i>	27	1	-	3.7%	-	Dudley & Vermeij, 1978
<i>T. communis</i>	26	7	-	27.7%	-	Dudley & Vermeij, 1978
<i>T. communis</i>	30	1	-	3.3%	-	Dudley & Vermeij, 1978
<i>T. communis</i>	9	0	-	0%	-	Dudley & Vermeij, 1978
<i>T. variegata</i>	11	0	-	0%	-	Dudley & Vermeij, 1978
<i>T. nodulosa</i>	116	32	-	27.6%	-	Dudley & Vermeij, 1978
<i>T. acropora</i>	13	2	-	15.4%	-	Dudley & Vermeij, 1978
<i>T. acropora</i>	22	0	-	0%	-	Dudley & Vermeij, 1978
<i>T. terebra</i>	33	5	-	15.2%	-	Dudley & Vermeij, 1978
<i>T. terebra</i>	18	5	-	27.8%	-	Dudley & Vermeij, 1978

(continues)

(continued)

Family Turritellidae	n	No of drill holes	No of repear scar	DF (%)	PF	Authors
<i>T. terebra</i>	12	2	-	16.7%	-	Dudley & Vermeij, 1978
<i>T. duplicata</i>	39	2	-	5.2%	-	Dudley & Vermeij, 1978
<i>T. sp.</i>	27	10	-	37%	-	Dudley & Vermeij, 1978
<i>T. leucostom</i>	156	80	-	51.3%	-	Tull & Bohning-Gaese, 1993
<i>T. gonostom</i>	172	5	-	2.9%	-	Tull & Bohning-Gaese, 1993
<i>T. acropora</i>	6	1	-	12%	-	Dudley & Vermeij, 1978
<i>T. annulata</i>	436	173	-	62.6%	-	Buchanan, 1958
<i>T. banksi</i>	12	2	-	16.7%	-	Dudley &Vermeij, 1978
<i>T. banksi</i>	9	0	-	0%	-	Dudley &Vermeij, 1978
<i>T. carinifera</i>	13	0	-	0%	-	Dudley &Vermeij, 1978
<i>T. communis</i>	15	3	-	20%	-	Dudley &Vermeij, 1978
<i>T. exoleta</i>	48	2	-	4.3%	-	Dudley & Vermeij, 1978
<i>T. gonostoma</i>	70	28	-	40%	-	Dudley & Vermeij, 1978
<i>T. leucostoma</i>	35	9	-	26%	-	Dudley & Vermeij, 1978
<i>T. mariana</i>	36	13	-	36%	-	Dudley & Vermeij, 1978
<i>T. nodulosa</i>	35	8	-	22.9%	-	Dudley & Vermeij, 1978
<i>T. pagoda</i>	50	1	-	2%	-	Dudley & Vermeij, 1978
<i>T. symmetrica</i>	57	11	-	19.3%	-	Dudley & Vermeij, 1978
<i>T. triplicata</i>	34	16	-	47.1%	-	Dudley & Vermeij, 1978
<i>T. variegata</i>	42	15	-	35.7%	-	Dudley & Vermeij, 1978
<i>T. sp.</i>	47	9	-	19.1%	-	Dudley & Vermeij, 1978
<i>T. sp.</i>	138	94	-	68.1%	-	Dudley & Vermeij, 1978
<i>T. sp.</i>	61	6	-	9.8%	-	Dudley & Vermeij, 1978
<i>T. communis</i>	2,209	973	-	44%	-	Sawyer & Zuchin, 2010
<i>T. gonostoma</i>	107	-	94	-	0.88	Gerhard et al., 1997
Total	5,640	1,729	2,562	31%	1.71	